A TAXONOMIC AND NOMENCLATURAL ASSESSMENT OF THE SPECIES OF *LIAGORA* (RHODOPHYTA, NEMALIALES) IN THE HERBARIUM OF LAMOUROUX

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ABSTRACT - In 1812 when J.V.F. Lamouroux named the genus *Liagora*, no species were described, but two taxa, *Fucus lichenoides* of Esper and *F. viscidus* Forsskal were listed, along with three undescribed species, *Liagora subulata*, *L. aegyptiaca* and *L. grisea*. In 1816, Lamouroux described seven species: *L. versicolor*, *L. ceranoides*, *L. physcioides*, *L. aurantiaca*, *L. farinosa*, *L. albicans* and *L. distenta*, all but the last as new species. *L. distenta* was based upon *Fucus distentus* Mertens ex Roth.

L. aurantiaca represents the basal portion of a hydroid. Of the remaining six species, *L. physcioides* and *L. versicolor* are conspecific with *L. distenta*. A study of 29 taxa shows that they have the anatomical characteristics of the following Lamouroux species: *L. distenta* (2 species), *L. ceranoides* (11 taxa); *L. albicans* (4 species) and *L. farinosa* (12 taxa). One further species, *L. articulata* was described by Lamouroux in 1821, but I have been unable to locate a specimen of it.

RÉSUMÉ - Quand J.V.F. Lamouroux dénomma en 1812 le genre *Liagora*, aucune espèce n'était décrite, mais deux taxa, *Fucus lichenoides* d'Esper et *F. viscidus* Forsskal étaient cités, ainsi que trois espèces non décrites, *Liagora subulata*, *L. aegyptiaca* et *L. grisea*. En 1816 Lamouroux décrivit sept espèces: *L. versicolor*, *L. ceranoides*, *L. physcioides*, *L. aurantiaca*, *L. farinosa*, *L. albicans* et *L. distenta*; toutes, sauf la dernière, sont des nouvelles espèces. *L. distenta* était fondée sur *Fucus distentus* Mertens ex Roth.

L. aurantiaca représente la portion basale d'un hydroïde. Des six espèces restantes, *L. physcioides* et *L. versicolor* sont conspécifiques de *L. distenta*. L'étude de 29 taxa montre qu'ils possèdent les caractères anatomiques propres aux espèces suivantes de Lamouroux: *L. distenta* (2 espèces), *L. ceranoides* (11 taxa), *L. albicans* (4 espèces) et *L. farinosa* (12 taxa). Une dernière espèce *L. articulata* a été décrite par Lamouroux en 1821, mais il n'a pas été possible de localiser de spécimen de celle-ci. (traduit par la rédaction).

KEY WORDS : Lamouroux, *Liagora*, Rhodophyta, taxonomy, type specimens.

INTRODUCTION

Liagora (Liagoraceae [= Helminthocladiaceae]) was first described by Lamouroux (1812, p. 185) as a member of his second family of flexible "zoophytes (animal-plants) or corals not entirely stoney". Among the genera named by him and placed with *Liagora* were invertebrate animals known currently as *Aglaophenia* and *Sertularia* (Class Hydrozoa). In 1816, Lamouroux published detailed descriptions of these zoophytes and included seven species in *Liagora*. Here, he remarked upon the resemblance of these taxa to lichens, some of them, however, retaining a gelatinous nature when living, which he thought was a characteristic of animals. Fortunately, the collections of Lamouroux were carefully preserved and are available for study at the Laboratoire d'Algologie, Université de Caen. In addition to examining specimens in this valuable herbarium, in 1963 I received the inestimable help of Roger Meslin who at that time was curator of the Chauvin Herbarium at Archives de Botanique, Caen and who was able to pinpoint specimens in the collections of Lamouroux and Chauvin, which aided the current study enormously.

There are many species of *Liagora* that have been described since Lamouroux (1816) named seven of them. As a result of a long-term study of this genus, (e.g., Abbott 1945, 1967, 1970, 1984; Abbott & Doty, 1960; Abbott & Yoshizaki, 1982) most of the more than 80 species now included in the genus have been examined and reviewed. This paper examines the specimens of the species of Lamouroux (1816) found in his herbarium (CN) and the types of 27 other taxa from other herbaria, which results in the reduction of the 27 to four Lamourouxian species. A second study that evaluates the species of *Liagora* accepted by J. Agardh (1896) has been submitted elsewhere.

MATERIALS AND METHODS

Herbarium material was photographed to show specimen habits, and small pieces (less than 4mm long) of each plant were prepared for light microscope examination, first by decalcifying in 10% acetic acid, then following the techniques described by Tsuda & Abbott (1985). I believe that the large number of conspecific taxa that have been described in *Liagora* has resulted from an examination of too few specimens and a lack of anatomical comparisons. Fresh material, used to check against the herbarium specimens, was either fixed in 4-5% formalin/seawater, or in Karpetchenko solution before slides were made.

The illustrations concentrate on external differences shown by type (and sometimes the only available) specimens, as the aspects of size, frequency and orders of branching were usually the items previous workers used for recognition of taxa. Certain other specimens are illustrated and

compared to the type specimens when they are recognized as members of the same species.

Species of *Liagora* are presently identified mainly upon their anatomy, which while dependent to a degree upon the external form of the thallus, appears to be the more stable and critical of the features selected for taxonomy. The features are: the branching pattern of the assimilatory filaments, the shapes of the cells in these filaments; the sizes and shapes of cells of the medullary filaments and the uniformity or dissimilarity of the filaments in section; where and how spermatangia are located on terminal cells; where carpogonial branches are located, the number of cells in the carpogonial branch; some detail of gonimoblast initiation; the origin of the involucre, what sort of filaments are produced by the involucre, and how it affects the appearance of the finished cystocarp; whether or not the carposporangia are terminal only, or are in short chains, or further divided into tetraspores.

All taxa being placed in the synonymy of the four Lamourouxian species must show similar assimilatory filaments (sizes and shapes), similar arrangements of spermatangia or similar development of gonimoblasts in relationship to involucral filaments. Since these characteristics are internal and microscopic, decalcification, followed by staining and mounting the material on microscope slides are required, a technique apparently never used by early students of this group of algae.

An external feature that may be used in concert with the anatomical ones is the degree of calcification (less versus heavily calcified). Many species that are mucosoid when living (and thus appearing to be lightly calcified) may lose their mucosoid nature and appear heavily calcified when dried. *Dotyophycus*, a *Liagora* relative, is such a species. Its mucosoid nature was not mentioned by Abbott (1970) when it was first described since only preserved material was available at that time and mucus was not evident. Living material is slippery, but this feature is lost on drying. Many of the *Liagora* species named by J. Agardh (1890) were recognized on their branching paterns and degree of calcification, both features I have found to be unreliable.

There are hundreds of specimens of *Liagora* that still must be examined. Large herbaria have specimens of *Liagora*, most of them either unidentified, or incorrectly identified. Among them are many new species, which will be more easily identified when the limits of the taxa already described are understood.

In listing specimens, their whereabouts are indicated by the abbreviations given in Holmgren *et al.* (1974). The cited specimens without herbarium attribution are from my own collections, and they will be deposited in the B.P. Bishop Museum (BISH), Honolulu, and elsewhere as material permits. Slides for microscopic examination are retained in my collections.

OBSERVATIONS

Liagora distenta (Mertens) Lamouroux, Hist. polyp. corall. flex., p. 240, 1816. Basionym: *Fucus distentus* Mertens in Roth, Cat. Bot. 3, p. 103, pl. 2, 1806. (Figs. 1-11).
Liagora versicolor sensu Lamouroux, Hist. polyp. corall. flex., p. 237, 1816. (Figs. 1-10).
Liagora physcioides Lamouroux, Hist. polyp. corall. flex., p. 239, 1816.
Liagora complanata C. Agardh, Sp. Alg. p. 396, 1822.

The plants that I ascribe to this species, which was described by Lamouroux (1816) as having a terete axis, with turgid branches, may have a single percurrent axis (*L. versicolor* var. A, Figs. 1, 2, 4; var. B, Fig. 5) or several leading axes (*L. versicolor* var. A, fig. 3; *L. versicolor* var. B, fig. 7) dichotomously (*L. versicolor* var. B, Fig. 6; var. C, Figs. 8-10) to subdichotomously (*L. versicolor* var. A, Fig. 4, Fig. 7) branched, with at least two other orders of branching, the last tending to be needle-like (Figs. 1, 2) or spinous. The apices are frequently furcate (Figs. 9-11).

The plants are reddish brown, shiny when living, but drying to a dull surface, the branches collapsing owing to very little calcification. Frequently the main or leading axes are compressed upon drying, but the branches usually remain terete (*L. versicolor* varieties A, B). Internally, the medullary filaments are less than 20μm diam., more frequently less than 15μm, with relatively short assimilatory filaments rarely more than 100μm long with 4-5 dichotomies; the upper cells of the assimilatory filaments (up to 2 removed from the terminal cells) are nearly spherical, about 8μm diam., and only up to twice longer in the lower part of the filament; the cystocarps have a well-marked involucre of filaments, and very large carpospores, ca 13μm wide by 26-30μm long. The species is dioecious. Spermatangia occur at the tops of the terminal cells in pairs, one to several mother cells borne on each terminal cell.

Specimens examined: Lectotype selected: a specimen from the Bay of Cadiz collected by Mertens (BM); perhaps an isotype in Herb. Chauvin, Archive de Botanique, Caen, annotated by Mertens (R. Meslin, pers. comm.). The various specimens of *L. versicolor* in Herb. Lamouroux (CN), including those under varieties A, B, C (Figs. 1-10), of which some are cystocarpic, others spermatangial, and are otherwise microscopically similar to one another and to more recently collected material of *L. distenta* (Fig. 11). Among the specimens included in *L. versicolor* var. C, a small specimen of *L. viscida* was encountered. Although most of the specimens associated in packets or on sheets with these varieties can be confidently identified with *L. distenta* some of them lack collecting data while others are too fragmentary to permit dissection for critical examination. The lectotype material previously selected by R. Meslin of *L. physcioides* (CN) from the Mediterranean coast of Spain was also examined.

More recent specimens examined: CANCAP 3362, s. coast of Madeira, west of Funchal, Macaronesia, (L 984.7469); CANCAP 6321, north coast of Tenerife, Canary Islands, May 31, 1982 (L 984.8098); CANCAP 3161 (Fig. 11) east coast of Lanzarote, Macaronesia (BISH ex L).

Discussion - There is some confusion concerning *Liagora versicolor* variety B (Figs. 5-7) because of Lamouroux's association of his specimens with *Fucus lichenoides*, a name subsequently assigned to *Gracilaria*. The specimen (Fig. 7) which looks like a faded, old specimen of *Gracilaria*, upon examination shows the multiaxial nature of the medulla and filamentous branches of assimilatory filaments, similar to *Liagora distenta*. A note within the packet which is labeled *L. versicolor* var. B on the outside bears Lamouroux's handwriting "fucus lichenoides Desfontaines". According to P.C. Silva (pers. comm.) when Lamouroux (1812) named *Liagora* and included *Fucus lichenoides* Gmelin, Hist. Fucorum, p. 120, pl. 8, Figs. 1, 2 (1768) and *Fucus viscidus* Forsskal, Fl. Aegypt.-Arab. p. 193 (1775), he should have chosen the earlier epithet "lichenoides" to serve as the type of *Liagora* since Art. 63 of ICBN would acknowledge that these two legitimate names were included in the protologue, making *L. versicolor* superfluous and hence illegitimate. According to Art. 7.13, the type of *Liagora versicolor* is the type of *Fucus lichenoides* S.G. Gmelin, whatever that may be. In Dr. Silva's opinion, Gmelin's fig. 1 could be *Liagora*, while fig. 2 could "just as well be *Gracilaria*. Had Lamouroux named *Fucus viscidus* to *Liagora*, there would have been no confusion since this is a species of *Liagora* and was selected as the generitype by Abbott (1945).

An examination of each of the specimens in the Lamouroux herbarium showed that some specimens that have been placed with *L. versicolor* are other taxa, and my concept of this species is thus limited to those specimens that have been labeled in Lamouroux's hand. Only one specimen of five under variety C, for example, has a description in Lamouroux's hand (Fig. 8). Two other specimens are clearly not *L. distenta*, being short and stocky, and one is *L. tetrasporifera* Børgesen, that is known from the western Mediterranean and Macaronesia. (A specimen from the Lamarck herbarium (in PC) is also *L. tetrasporifera* and may have been collected at the same time).

DeToni (1897) placed *L. complanata* C. Agardh in synonymy with *L. distenta*, an opinion with which I agree upon examining the specimens in LD.

Lamouroux (1816, p. 241) recognized *L. distenta* as a species "very distinct from the numerous varieties of *L. versicolor* ", although the main distinction that he offered was a compressed frond for *L. versicolor*, and terete or cylindrical for *L. distenta*. His descriptions of their branching patterns appear to be more or less similar, and both species have furcate apices. Although color is not mentioned in his description of *L. distenta*, he devoted many lines to the many colors of *L. versicolor*, "le *Liagora* a plusieurs cou-

leurs". Examination of modern specimens of *L. distenta* shows a range from rusty through several shades of brownish red to greenish brown; old specimens, however, like those of Lamouroux's *L. versicolor* are faded to a cream color. The specific epithets may give a clue as to the level of examination: *physcioides* (like the lichen genus *Physcia*), perhaps implying greyish-white and flat; and *complanata*, meaning flattened or compressed, whereas *distenta* (Mertens' descriptor) means swollen or bulging. Thus, none of these descriptors would qualify for the taxonomic features now used; those now recognized such as assimilatory filaments, male and female reproductive structures are alike in these taxa.

Liagora distenta is not well known among *Liagora* species, owing to its relatively restricted distribution in the Mediterranean and Macaronesia (Børgesen, 1927 and Leiden herb.). It is less common in the western Mediterranean (Feldmann, 1942, p. 222) than *L. viscida* and differs externally principally in its reddish brown color, and the very fine ultimate branchlets, which are less than 1mm diam. Because of the relatively narrow distribution of *L. distenta*, records from the Caribbean (Mazé & Schramm, 1878) or the Pacific (Harvey, 1855) are viewed with suspicion, and specimens upon which this identification was made must be re-examined. R. Meslin (pers. comm. Aug., 1963) suggested that Lamouroux probably viewed the Mertens specimen in the Chauvin herbarium, as the two naturalists frequently exchanged specimens. The Lamouroux herbarium (CN) does not contain a specimen of *L. distenta* under that name.

I have not had experience with either *L. viscida* or *L. distenta* in the field, nor have I examined large numbers of specimens as I have with most other taxa, but it would not surprise me if these two taxa were combined in some future study. Except for being monoecious and possessing a conspicuous involucre, *L. viscida* does not appear to be significantly different from *L. distenta*. I have commented upon the relatively large carposporangia of the latter species, but should *L. viscida* demonstrate them also, the two species should be re-evaluated at that time. Some species, e. g., *L. albicans* (see below), can be either monoecious or dioecious.

Liagora ceranoides Lamouroux, Hist. polyp. corall. flex., p. 239, 1816. *Non L. ceranoides sensu* C. Agardh, Sp. Alg. p. 396, 1822. *Non L. ceranoides sensu* Zanardini, Iconogr. phycol. adriat. pl. 102, figs. 4-5, 1874. (Figs. 12-15).

Liagora pulverulenta C. Agardh, Sp. Alg. p. 396, 1822.

Liagora pulverulenta var. *compacta* Weber van Bosse, Siboga Exped. vol. 59: 199, fig. 61, 1921.

Liagora leprosa J. Agardh, Öfv. Kongl. Vet.-Akad. Förh. 4: 8, 1847.(Fig. 13).

Liagora subarticulata Grunow, J. Mus. Godeffroy [Hamburg] 3: 35, 1874.

Liagora patens Crouan et Crouan in Mazé et Schramm, Alg. Guadeloupe, p. 14, 1865.

Liagora prolifera Crouan et Crouan in Mazé et Schramm, Alg. Guadeloupe, ed. 2 p. 185, 1878.
Liagora opposita J. Agardh, Anal. Alg. Cont. 3: 101, 1896. (Fig. 14).
Liagora subpaniculata Butters, Minn. Bot. Stud. 4: 168, pl. 24, fig. 7, 1911.
Liagora tildeniae Butters ["tildenii"], Minn. Bot. Stud. 4: 171-172, pl. 24, fig. 11-12, 1911.
Liagora tildeniae ["tildenii"] var. *lubrica* Butters, Minn. Bot. Stud. 4: p. 172-173, pl. 24, fig. 13, 1911.
Liagora pilgeriana Zeh, Notizbl. K. Bot. Gart. Berlin 5: 272, 1912.

Plants are usually short, typically 3-4cm tall, but are occasionally up to 8cm, and dichotomously to fastigiately branched, the axes ca 1mm diam. throughout; branching is crowded toward apices, and the segments short; mid-portions of axes are without branches but with proliferations (f. *ceranoides*) (Figs. 12, 15) or branched and without proliferations (f. *leprosa*) (Fig. 13). Living thalli are gray-white with pink apices, slippery owing to mucus, drying to white or gray with pink showing through, with calcification powdery (farinaceous or pulverulent), except for apices which are brownish red and protrude with little or no calcification.

Internally, the medulla is between 0.35 and 0.6mm thick, with several kinds of medullary filaments: slender, less than 18μm diam. by 4-5 times longer; irregular shaped, from ca 40μm diam., tapering to 13μm, and (in older portions) cylindrical with rounded ends, between 20-30μm diam. Bases of assimilatory filaments usually produce one to five long rhizoidal filaments paralleling the axis; some of these may later form erect, assimilatory filaments shorter and with fewer branches than the cluster from which the rhizoid started. The lower half of the assimilatory filaments consists of elongate oval cells, attenuate at each end, 26-52μm long for the first two dichotomies, gradually becoming shorter, and the last (4th or 5th) dichotomy having cells nearly spherical, about 4μm, dividing within every cell or every other cell, forming crowded terminal clusters. Hairs commonly occur on the terminal cells.

The species is dioecious. Carpogonial branches occur at the second dichotomy from the base of the assimilatory filaments, are attached at the midlateral face of the bearing cell, or slightly higher, are curved, and of 3-4 cells. This position requires the trichogyne to elongate 150-160μm to clear the top of the cortex. The mature cystocarp is 0.5mm across in polar view, including the conspicuous involucre, whose filaments are usually unbranched and the cells bead-like. The gonimoblast itself is about 225μm diam. in polar view. Carpospores are ca 4 x 6μm, usually in short rows of 2-3 cells, the spores produced singly from the terminal cell. Spermatangia are densely formed and occur on stalks (spermatangial mother cells) on the small terminal cells of the assimilatory filaments.

Specimens examined: Holotype: *L. ceranoides* (Fig. 12) from St. Thomas, Virgin Islands (CN), a spermatangial plant; holotype of *L. leprosa* (Fig. 13) from Vera Cruz, Mexico, leg. Liebmann (LD 32285; isotype in C), both are

spermatangial plants; lectotype selected: *L. opposita* (Fig. 14) from Florida, leg. Curtiss (LD 32296), a cystocarpic plant; holotype of *L. subarticulata* from Ovalau, Fiji, leg. E. Graefe (PC), a cystocarpic plant; holotype of *L. pilgeriana* from Rio de Janeiro, leg. A. Glaziou 5689 (BM), a cystocarpic plant; holotype: *L. pulverulenta* var. *compacta* from Macassar (L 941.98.130); holotype of *L. subpaniculata*, dredged off Kauai I., Hawaii by U.S. Fish Comm. No. 4023 (MIN); holotype: *L. patens* from Pointe-à-Pitre, Guadeloupe, Mazé & Schramm No. 1492 (BM). These eight specimens all have assimilatory filaments that are divided near the top, and large cystocarps with slender gonimoblast cells and small carposporangia, surrounded by a conspicuous involucre; there are also rhizoidal filaments near the bases of the assimilatory filaments. The spermatangial plants that comprise the holotypes of *L. ceranoides* and *L. leprosa* show spermatangia attached by mother cells to ultimate and penultimate cortical cells, creating haloes around each of the bearing cells. Their arrangement gives the otherwise insignificant sizes of the spermatangia a conspicuous quality that is lacking in most species of subgenus *Liagora*.

Other specimens examined of *L. ceranoides* f. *ceranoides*: LD 32297 (among specimens of *L. tenuis*, although labelled *L. pulverulenta* in the handwriting of J. Agardh); Abbott 15660, Coney I., Bermuda, ca 2m depth, strong tidal current through entrance to Castle Harbor, leg. John Schwede, June 11, 1981; Gittins 7584, Playa de Tamarindo, Bahia de la Ballena, Puerto Rico, at 1m depth (BISH); CANCAP 6466, Santiago Ilha de Santa Maria, Cape Verde Islands (L 984.7948); Abbott 11939, Light Princess, St. Croix, Virgin Islands (Fig. 15, which resembles the holotype of *L. ceranoides*); Abbott 11796, Boiler Bay, St Croix, leg. D.P. Abbott, Jan. 1, 1974; Abbott 18646, on small rocks 0.5m depth, Kahala, Hawaii, leg. Shawn P. Carper, April 17, 1988; Abbott 1344, Laie Bay, Hawaii, 5 May 1946 (Fig. 16, which resembles the holotype *L. opposita*). *L. ceranoides* f. *leprosa*: LD 32283 from St. Thomas, Virgin Islands, as *L. leprosa*; LD 32286 from Garden Key, Florida and LD 32287 from Sand Key, Florida, both as *L. leprosa*; Abbott 13457 (Fig. 17, which resembles the holotype of *L. leprosa*), from Hundred Islands, Philippine Islands.

Discussion. - Yamada's (1938) formae may be accepted as useful in designating at least two habits. *L. ceranoides* α *pulverulenta* (C. Agardh) Yamada (which should be called *L. ceranoides* forma *ceranoides*) is described as having many short proliferations represented on the holotype (CN), and *L. ceranoides* forma *leprosa* (J. Agardh) Yamada (Yamada, 1938, as *β leprosa*), which lacks them. The holotype of *L. ceranoides* is from St. Thomas, Virgin Islands, and it is for this reason that the detailed description of Børgesen (1915-20) of *L. pulverulenta*, based upon material from St. Croix and St John which are adjacent to St. Thomas, should be carefully studied. Many specimens are encountered that are not as clear-cut as the ones illustrated here; generally, the intergrades are found within populations.

The main features of *L. ceranoides* are: the soft texture of the short living plants; the abundant rhizoids at the junction of the assimilatory filaments and the medullary filaments; the small, numerous cells in the gonimoblast filaments; the small size of the carposporangia, and the relatively large diameter of the involucre which bears slender filaments, and the short laterals or proliferations along the axes (as present in f. *ceranoides*). Within this characterization, *L. tildeniae* Butters and *L. tildeniae* var. *lubrica* Butters are placed in synonymy with *L. ceranoides* although no material is available in Herb. MIN. for comparison. Although Butters placed these two taxa in a new section of *Liagora* (Corymbosae), stating that they combined the medullary structure of *L. cheyneana* (= *L. farinosa*) with the cortical structure of *L. leprosa* (= *L. ceranoides*), the medullary characterization is not specific to *L. farinosa*. Moreover, the description and identification by Butters (1911, p. 171, pl. 24, fig. 10) of *L. corymbosa* from Hawaii does not match the lectotype of *L. corymbosa* (LD 32368), a fact that bears out the doubt he expressed in his identification. *L. corymbosa* J. Agardh is being placed in synonymy with *L. farinosa* Lamour. in this paper. *L. corymbosa* of Butters is identified with *L. fragilis* Zanardini.

Of the taxa being placed in synonymy, the names of five (*subarticulata*, *patens*, *opposita*, *prolifera*, *subpaniculata*) apply to branching patterns, and three taxa, named after persons (*tildeniae*, *tildeniae* var. *lubrica*, and *pilgeriana*) are also distinguished on their branching patterns (Butters, 1912, p. 171, and Zeh, 1912, p. 273). Butters (1912, pl. iv, figs. 11-13) illustrates the assimilatory filaments of specimens I would associate with *L. ceranoides*. The remaining taxa (*pulverulenta* and *leprosa*) are named for the texture of the calcification on the surface of the thalli. Neither branching patterns nor surface structure are primary features of *L. ceranoides*; all specimens show the internal anatomy referred to above.

Liagora albicans Lamouroux, Hist. polyp. corall. flex. p. 240, pl. 7, fig. 7, 1816. (Figs. 16-21).

Liagora decussata Montagne, Ann. Sci. Nat. Bot., ser. 3, 11: 64, 1849. (Fig. 17).

Liagora maxima Butters, Minn. Bot. Stud. 4: 165, pl. 24, figs. 3-5, 1911. (Figs. 19-21). *L. decussata* of Tilden, 1902, p. 106, *non* Montagne.

Liagora erecta Zeh, Notizbl. Bot. Gart. Berlin 5: 268, 1912.

Liagora ceylonica Zeh, Notizbl. Bot. Gart. Berlin 5: 268, 1912. (Fig. 18).

Intertidal plants are pinnately branched, with strongly percurrent axes (Fig. 19, 20), but subtidal plants (5m depth or more) favor dichotomous branching (Fig. 21). Branchlets are usually tapering or acuminate (a feature rare in *Liagora*). A tenacious disk-shaped holdfast which may be up to 0.5cm diam. gives rise to fronds up to 45cm tall, with terete branches, from 2 to 5mm thick. Calcification is usually thick and brittle, the plants completely white, or white and pink or green, or reddish, with gelatinous tips;

occasionally intertidal plants show sections of the axes with only the medulla apparent, owing to abrasion. Subtidal plants are strongly annulate.

Vegetative cells of female gametophytes are as much as 30% broader and longer than those of male gametophytes. Assimilatory filaments are dichotomously branched, the lower cells cylindrical to rhomboid, their diameter less than 8μm, becoming oval toward the top, frequently with terminal cells somewhat inflated or slightly broader than penultimate cells, ca 5μm diam. by 10μm long and frequently tear-drop shaped, 2 or 3 are attached to the penultimate cells. In surface view, terminal cells are frequently at right angles to each other. They frequently have 1-3 delicate hairs, or scar cells of hairs. The shape of the cells of the lower portions of the assimilatory filaments in the two gametophytes may differ, the cells being less rhomboid and more oval in the female plants.

Carpogonial branches are 2-4 cells long, and are attached on the lateral face of the bearing cell. The involucre is initiated before the first division of the zygote nucleus and arises from cells and filaments below and adjacent to the carpogonial branch. Involucral cells are slender, less than 2μm diam. The basal cells of involucral filaments become entangled below the gonimoblast and form a tight group difficult to squash. The cystocarp is ca 250μm diam. in polar view, with the bulk of the cells sterile, the terminal two in each filament becoming 2arposporangia in turn, ca 5-9μm diam., 8-10μm long. As the gonimoblast matures, the contents of cells of the carpogonial branch, the bearing cell, as well as some neighbouring cells become fused.

The species is usually dioecious. Spermatangia occur in short finger-like clusters singly or in 2's or 3's from spermatangial mother cells occurring on ultimate and penultimate cells. Spermatangia and their mother cells are ca 2μm diam.

Specimens examined: A small specimen only 3cm tall (CN) with Lamouroux's description of *Liagora canescens* written under it must serve as the holotype. *L. canescens* is not a species but a name used in error on the caption to pl. VII as well as on this specimen; both in the text and index, *L. albicans* is used. This specimen is cystocarpic and labelled as from Indes Orientales. In the Chauvin herbarium, there are several specimens labelled *L. albicans*. There are two specimens on one sheet; the one on the right (Fig. 16) is monoecious with irregular, finger-like spermatangia, and cystocarps with involucral filaments formed early. A 3-4 celled carpogonial branch is borne at the mid-level of the assimilatory filaments, attached to the lateral face of the bearing cell. Since this specimen is monoecious and the portion of the holotype examined is cystocarpic only, these may not be from the same collection. Another specimen in Herb. Chauvin is a large plant 10cm high with pinnate branches; it has large cystocarps with a lightly developed involucre. The Lamouroux herbarium has a second specimen in a packet

which has four main pinnately divided fronds, the longest 9cm. It is spermatangial. Thus, among these old materials, there are specimens that are monoecious, and others that are dioecious, which are conditions found in living populations.

Other type material examined: the holotype (Fig. 19) of *L. decussata* from San Antonii (Saint Vincent?), Cape Verde Is., leg. Forbes in Montagne herb. (PC); the holotype of *L. erecta* Zeh leg. Thurston No. 82, Feb. 1900 from Madras, India (BM); lectotype selected of *L. maxima* Butters, Tilden no. 418 from "2 miles north of Waianae, Oahu" (Hawaii), June 12, 1900 (MIN); holotype (Fig. 20) of *L. ceylonica* Zeh. Ferguson No. 30/4 from Ceylon (BM). Other specimens examined: (as *L. erecta*) from Mahabalipuram, India, leg. M.O.P. Iyengar (C); Ferguson 30/4 subnomine *L. pulverulenta* from Ceylon (C); (as *L. decussata*): from St. Nicholas Calonde, Playa de Prainha, Cape Verde, leg. C. Bolle, 1859 (Montagne herb., PC); from the same place, spermatangial, leg. Piccone, 1851 (PC, VER); from Guadeloupe Is. leg. G. Hamel (UC 687762); from Riambel, Mauritius leg. R.E. Vaughan (C); from Taiwan (Formosa), (SAP, a specimen collected at Taito by Y. Yamada, April 18, 1934). Hawaiian Islands: Tilden 983, 1564 (as *L. decussata*) in American Algae Century V (UC, MIN, FIELD, BISH); (as *L. maxima*) Oahu Island at Maili, Papenfuss 10450 (UC); at Makua (Fig. 21), between 8-9m depth, July 16, 1983, McDermid 469; at Kahanahaiki, Abbott 16450, (Fig. 20), leg. D.P. Abbott & I.A. Abbott, April 1, 1984; Abbott 16276 (Fig. 19), Pupukea, leg. Vernon Sato, May 15, 1983 (BISH). Maui Island, Kainalimu Bay, March 30, 1984, leg. K. McDermid. Hawaii Island, Abbott 17189, from Puuhonua National Monument, Honaunau, leg. W.H. Magruder March 17-23, 1985; Abbott 18708, near Keahole Point, Kona, intertidal, leg. W.H. Magruder April 19, 1988 (Fig. 22).

Discussion. - The plants that have been known as *Liagora erecta* or *L. ceylonica* (Fig. 18) show strong percurrent axes, whereas most plants determined as *L. decussata* (e.g., UC 111797 from Hope Bay, Jamaica) are pinnately branched, forming relatively dense bushes (Fig. 21), the axes thus becoming obscure. The Montagne material (PC) shows the holotype with elongate, percurrent axes, while other material identified by Montagne (but not collected with the holotype of *L. decussata*) are bushy plants. Specimens of *L. maxima* show both types of branching and intermediates (Figs. 21-23). A second specimen (not the holotype) of *L. albicans* (CN) has a percurrent axis and may be a part of a plant, or the whole plant; the holdfast is lacking.

The fact that only a few specimens of *L. decussata*, *L. erecta* and *L. maxima* are found in herbaria (except for the last, in Bishop Museum) may indicate that the species is not common. In Hawaii, the species is a relatively strict spring annual, appearing about the end of March on basalt boulders and eroded coral, and disappearing by mid-June, persisting at 5-6m depth into late July. Where it occurs, it is common to abundant for that short pe-

riod; the plants are conspicuous because they are frequently at the +0.1 ft tidal level, and therefore out of water during many low-water periods. Two features about the plants may reflect these drying-out periods: (1) the brittle calcified layers (and the assimilatory filaments which are enclosed by these layers) frequently break off, leaving bare spaces along the axes and branches (Fig. 23); (2) on making squash preparations of the thalli, thin sections must be cut after decalcification, and laid on their faces, for pieces longer than 2-3mm cannot be squashed effectively owing to their cartilaginous consistency.

Balakrishnan (1955) provided an excellent account of post-fertilization events in *L. albicans* (as *L. erecta*) from India and suggested that upon comparison with what had been published on *L. maxima* (Abbott, 1945), it might be that the two species were identical. One of the features that he showed, and which I confirm, is a large post-fertilization fusion cell that involves all cells of the carpogonial branch, extending to adjoining cells and filaments. Very few species of *Liagora* show such conspicuous fusion.

The specimen that Yamada (1938, pl. 7, textfigs. 13-14) used to illustrate *L. decussata* which he identified from Formosa (Taiwan) has been examined and I believe that it is identical with the material that is being identified as *L. albicans* in this paper. Yamada (1938, p. 23) was the first to point out the cluster of entangled filaments at the base of the cystocarp, which is a useful and unique feature that should be searched for in cystocarpic plants. The type specimens of the four species placed in synonymy strongly resemble one another and *L. albicans* in their percurrent axes and pinnate-paniculate branching patterns; the dichotomously branched specimens that also are included in the species description are not shown by these specimens. Whatever the branching pattern, the anatomical details are similar whether the plants are monoecious or dioecious.

Liagora aurantiaca Lamouroux, Hist. polyp. corall. flex., p. 239-240, 1816. (Fig. 22).

The specimen (Fig. 22) in the Lamouroux herbarium (CN) consists of the chitinous stoloniferous portions of a hydroid, possibly *Aglaophenia*.

Liagora farinosa Lamouroux, Hist. polyp. corall. flex. p. 240, 1816. (Figs. 23-29).

Liagora hirta Harvey et Bailey, Proc. Boston Soc. Nat. Hist. 3: 373,1851.

Liagora cheyneana Harvey, Trans. Roy. Irish Acad. 22 (Sci.): 552, 1855.

Liagora elongata Zanardini, Flora 34: 35, 1851; Mem. dell' Ist. Ven. p. 274, pl. 6, fig. 1, 1857.

Liagora crassa Dickie, J. Linn. Soc., Bot. 14: 195, 1874. *Non L. crassa* Levring, Ark. Bot. ser. 2, 2: 502, 1953, a later homonym [Art. 64, ICBN]. (Fig. 27).

Liagora hirida Dickie, J. Linn. Soc., Bot. 14: 195, 1874.

Liagora preissii Sonder var. *pacifica* Grunow, J. Mus. Godeffroy [Hamburg] 3: 36, 1874.

L. cayohuesonica Melvill, [Trimen] J. Bot. 13: 262, 1875. (Fig. 25).
Liagora farionicolor Melvill, [Trimen] J. Bot. 13: 263, 1875.
Liagora bipinnata Crouan et Crouan in Mazé & Schramm, Alg. Guadeloupe, ed. 2, p. 183, 1878.
Liagora corymbosa J. Agardh, Anal. Alg. Cont. 3, p. 104, 1896. (Fig. 28).
Liagora cliftonii (Harvey) J. Agardh. Sp. Alg./ 3 (1): 515, 1876. Basionym:*Galaxaura cliftonii* Harvey. Phyc. austr. pl. 275, 1863. (Fig. 24).
Liagora paniculata J. Agardh. Anal. Alg. Cont. 3, p. 106. (Fig. 29).

Plants occur in at least three morphotypes: 1) saxicolous or epiphytic, 6-9cm tall, loosely dichotomously branched, with axes and branches no more than 1mm diam., branching frequent at tops, plants tan to reddish brown in color, sometimes drying greenish gray, with white tips; whole thallus, but especially apices mucosoid (Figs. 24-25, similar to *L. cliftonii* and *L. cayohuesonica*); 2) plants are 8-13cm tall, primary axes are 1-3mm diam., with or without proliferations interrupting a subdichotomous branching pattern; branches show 1.5-2.5cm intervals between divisions, their apices forming a corymbose outline. Examples are a specimen in Chauvin herbarium (possibly an isotype) with proliferations, which is probably the larger part of the holotype (CN) of *L. farinosa* (Fig. 23), and the illustration of *L. elongata* by Zanardini (1857, pl. 6, fig. 1), without proliferations; 3) plants are up to 30cm tall, with coarse primary axes percurrent, 4-5mm diam., frequently compressed; branches are divided once or twice pinnately, with segments 2-3mm diam., 2-7cm long. Examples of this form are the isotype specimen of *L. farinosa* f. *pinnatiramosa* Yamada (Fig. 29) and the holotype of *L. crassa* Dickie (Fig. 27).

Internally, all plants have medullary filaments 40-70μm diam. by 2.5 to 3 times longer, which are somewhat sausage shaped (narrower at each end than in the middle). The assimilatory filaments have a primary site of branching on the lowest cell cut off from the medulla, usually two, but occasionally three branches arise from the distal end of this cell, each in turn dividing subdichotomously and forming parallel filaments. Assimilatory filaments of spermatangial plants show a regularity of dichotomous or subdichotomous branching, with the final dichotomies near the top more numerous than on female plants; the female plants have assimilatory filaments with an irregularly branching pattern-usually after the lowest dichotomy, the upward divisions are no longer dichotomous. Near the apices of the thalli, when young, the assimilatory filaments show cells that are a broad oval, with constrictions between them; in older portions of the thalli, the lower cells of the assimilatory filaments may retain their oval shapes, ca 15μm diam. by 40μm long, but the upper cells become broader, up to ca 20μm diam. by 26μm long, and are characterized by relatively straight cell walls with no constrictions. The latter subcylindrical to cylindrical cells of assimilatory filaments are characteristic of more mature portions of this species.

Carpogonial branches are of 4-5 cells and are borne low in the branching system, on assimilatory branchlets of the first, second, or third order

(Abbott, 1984). They may be attached laterally or from their bases to the bearing cell, and may be a little bent in the first case, or straight in the second. Rarely, two to four carpogonial branches are borne in the same cluster. The ensuing gonimoblast may have a small number of sterile filaments below it, arising from adjacent assimilatory filaments. The assimilatory filament branches that are below the cystocarp are deflected around it; they may be misidentified as an involucre. Cystocarps are small, 150-300μm across, with carposporangia 15-18μm diam. by 38-41μm long, tear-drop shaped. The plants are dioecious, rarely monoecious. The spermatangia are the clearest taxonomic feature of this species, as they are borne in a very dense, massive head or cluster, and may cover the top 1-3 cells of the assimilatory filaments. The early illustration of Zanardini (1857) showing these characteristic spermatangia in *L. elongata* leaves no doubt that this species is synonymous with *L. farinosa*. Monosporangia are also known (Abbott, 1945).

Specimens examined: Holotype (Fig. 23) in Lamouroux herbarium (CN), a slender specimen with branches no more than 1mm wide. It bears a description in Lamouroux' hand. This appears to be a branch of a specimen in the Chauvin herbarium which is a larger plant complete with holdfast. An additional plant, stamped Herbarium Lamouroux, completes the CN holdings on *L.farinosa*. All three came from the Red Sea ("Aegypte") in the vicinity of Suez, collected by Delile. A presumed isotype is in the Thuret herbarium (PC), identified by Lamouroux and labelled as collected by Delile in the Red Sea.

The type specimens of all of the 12 synonyms of *L. farinosa* that are listed have been examined: holotype of *L. hirta* from Navigator's Islands (BM); holotype of *L. elongata* ex Herb. Zanardini leg. Portier from the Red Sea (L 941.149.388), a spermatangial plant; isotype (L 941.149.491), both numbers with numerous "monosporangial discs"; lectotype selected of *L. cheyneana* from Cape Riche, western Australia (BM), a spermatangial plant; isotypes in L 941.149.238; holotype (Fig. 27) of *L. crassa* from Flat Island, Mauritius leg. Robilard (BM), cystocarpic; holotype of *L. lurida* from Mauritius leg. Pike (BM), cystocarpic; lectotype of *L. bipinnata* from Pointe-à-Pitre (Ilet Boissard), Guadeloupe, Mazé no. 947 (BM); lectotype of *L. preissii* var. *pacifica* from Ovalau, Fiji (PC), spermatangial; isotype, L 941.149.231; holotypes of *L. cayohuesonica* (Fig. 25) and *L. farionicolor* from Key West, Florida (both BM), both cystocarpic; lectotype of *L. corymbosa* (Fig. 28) from Florida (LD 32368), cystocarpic; holotype (Fig. 24) of *L. cliftonii* from Swan River, Australia leg. G. Clifton (BM), spermatangial; holotype (Fig. 32) of *L. paniculata* from Florida (LD 32395), cystocarpic.

Other specimens examined (BISH, from which cell shapes and measurements were taken, and reproductive elements assessed): Abbott 10830, (monoecious), Red Sea, Al Ghardaga, northwest Gulf of Suez, June 10, 1967, leg. John Pearse. (The Red Sea is the type locality of *L. elongata* Zanardini,

and the type locality of *L. farinosa*). Hawaiian Islands: Abbott 18813, Kailua Oahu, leg. I. Abbott, June 25, 1988; Abbott 1475, Hauula, Oahu, leg. I. Abbott, May 30, 1946; Abbott 16311b, Pupukea, Oahu, leg. K. McDermid, May 21, 1983; Abbott 13462, Laysan Island, leg. Fred Ball, July 13, 1977. Other localities: Abbott 14916, Santa Marta, Colombia, leg. G. Bula Meyer, May 20, 1978; Bermuda, leg. W.R. Taylor, 16 April 1949; St. Catherine's Fort, Bermuda, leg. L.R. Blinks, May 6, 1970; Abbott 13767 (Fig. 37), 1.5m depth near Bahia Honda Bridge, West Summerland Key, Florida, leg. John Schwede, April 20, 1980; CANCAP 2, no. 26, Canary Islands, Aug. 24, 1977 (BISH, ex L); Barkley Sound, Mauritius, leg. G. Morin, May 10, 1948, (BISH, ex C); Abbott 16393, Singapore, leg. R. Sellers, April 1977; Bonin Islands, Haja-jima leg. S. Segawa (as *L. farinosa* f. *pinnatiramosa*) Yamada (BISH ex SAP); Naha, Okinawa, leg. Y. Yamada.

Discussion: For a species that shows great variability in external form, *Liagora farinosa* seems to be reasonably uniform in its internal structure. It is clear that few have examined the material microscopically, and equally plain that the descriptions of the plants have not covered the entire range of branching patterns, sizes, thickness of branches, or variation in color. Lamouroux (1816) was correct in stating that the plants dry to an olive green, as this is true of perhaps 25% of them; more commonly they are a reddish tan color; rarely are they white on a herbarium sheet, as the majority of specimens of *Liagora* are. The large number of illustrations of the habits shown here are necessary to show the variability in this species. Of the 14 taxa involved, five were named for branching patterns (*elongata, crassa, bipinnata, corymbosa, paniculata*) while three were named for persons (*cliftonii, preissii* and *cheyneana*) and branching patterns are mentioned in their descriptions. Two (*farinosa* and *hirta*) were named for surface structure, two for color (*lurida* and *farionicolor*. The type specimens of each of these species show assimilatory filaments as described for *L. farinosa* and either spermatangia or cystocarps as described for this species.

Howe (1920) placed in the synonymy of *L. farinosa* seven species: *L. elongata* Zanard., *L. cheyneana* Harv., *L. lurida* Dickie, *L. crassa* Dickie, *L. cayohuesonica* Melvill, *L. farionicolor* Melvill, and *L. corymbosa* J. Agardh. Yamada (1938) added *L. hirta* Harv. et Bail., Abbott (1945) added *L. preissii* var. *pacifica* Grun. and Levring (1953) added *L. cliftonii* (Harv.) J. Agardh. One other species is added in this paper, *L. bipinnata* P. et H. Crouan. Whether Howe examined specimens of the species he placed in synonymy is not known, but each has been examined for this study.

L. brachyclada of Crouan et Crouan in Mazé et Schramm, p. 184, 1878, *non* Decaisne, from Moule, Guadeloupe, Mazé no. 947 (BM) is *L. farinosa*. *L. paniculata* of Butters, 1911, p. 174, based on Heller no. 2132 from Hawaii is not *L. farinosa* but *L. papenfusii* Abbott (1945) which is not discussed in this paper.

Ganonema farinosum (Lamour.) Fan et Wang, Acta Phytotax. Sin. 12: 490-493, 1974 (basionym: *Liagora farinosa* Lamouroux, Hist. polyp. corall. flex., p. 239, 1816) and *G. pinnatiramosum* (Yamada) Fan et Wang, Acta Phytotax. Sin. 13 (2): 73, 1975, (basionym: *Liagora farinosa* f. *pinnatiramosa* Yamada, Sci. Pap. Inst. Alg. Res. Fac. Sci. Hokkaido Imp. Univ. 2: 26, pl. 10, 1938) (Fig. 26) are retained as *L. farinosa* by Abbott (1984). The main distinction of *Ganonema* was the formation of carpogonial branches on secondary (and tertiary) branchlets; Abbott (1984) showed that primary, secondary, and tertiary branches can bear carpogonial branches in this species, and that the location of these reproductive structures is not fixed in this or some other species of *Liagora*.

Galaxaura valida sensu Crouan et Crouan in Mazé & Schramm, Alg. Guadeloupe, ed. 2, p. 183, 1878, represented by a specimen (BM) from Saintes, Guadeloupe, No. 1850 of Mazé & Schramm is identified with *Liagora farinosa*. The basionym of *G. valida*, *Liagora valida* Harvey, does not in any way resemble *L. farinosa*; neither *Liagora* species resembles any species of *Galaxaura* that I know from the Caribbean.

Other names or taxa

1. *Liagora canescens* Lamouroux, Hist. corall. polyp. flex., pl. 7, fig. 7, 1816. This name, appearing on the holotype specimen and the illustration for *Liagora albicans*, was clearly a mistake for *Liagora albicans* which was described in the text.

2. *Liagora aegyptiaca*, named without description by Lamouroux (1812) was apparently a name that Lamouroux meant to use, but decided upon *Liagora farinosa* instead, since this name is written on the sheet bearing the holotype of *L. farinosa*, but not on the label bearing the description of the species. *L. grisea* is thought to be *L. farinosa* also, as few *Liagora* available to Lamouroux were gray in color.

3. *Liagora subulata*, named without description by Lamouroux (1812) was never further described; there are no specimens in CN bearing this word.

4. *Liagora articulata* Lamouroux, Expos. méth. gen. ordre Polyp. p. 19, pl. 68, fig. 9, 1821.

Aside from Lamouroux's description, which is not specific enough to aid in identification, this species has been cited in an article on *Liagora* by Deslongchamps (1825), by Chauvin (1842) and by Kützing (1849). The original specimen is not in the Lamouroux or Chauvin herbaria; it was from Ile de Bourbon (Réunion) and was sent to Lamouroux from the British Museum. I have not seen this specimen, and since this paper is based on an examination of specimens, I cannot comment on this species.

5. Liagora foeniculacea Lamouroux

This name is cited by Kützing (1849, p. 539) with the comment "Lamour. ex Chauv. Rech. p. 127" (Chauvin, 1842). There is no reference to this species in the Chauvin publication, nor in the paper by Deslongchamps (1825), nor in the papers of Lamouroux. Kützing (1849, p. 539) obviously made a mistake by giving Lamouroux as the author of this binomial; he probably meant Lamarck as the name *Liagora foeniculacea* (Lamarck) Blainville, Man. Actinol. p. 559, 1834 exists (P.C. Silva, pers. comm.). I have not seen any specimens of this species.

CONCLUSION

The four species treated in this study, *L. distenta* (Mertens) Lamour., *L. ceranoides* Lamour., *L. albicans* Lamour. and *L. farinosa* Lamour. show a larger number of habits than their holotypes or lectotypes demonstrate, but on the basis of anatomy, all have been placed in sections and groups (subsections) by Yamada (1938). Yamada's treatment of *Liagora* has been followed by subsequent workers tacitly or by implication, but they have not disturbed the subdivisions to which these four species can now be assigned. With the placing of 27 names in the synonymy of these four species, it is clear that changes will be made in Yamada's generic divisions. However, it is premature to make those changes now inasmuch as a large number of taxa is still under study. Following Yamada's classification (Yamada, 1938, p. 4), section Validae which is characterized by lateral carpogonial branches (Yamada, 1938, fig. 12a, b), assimilatory filaments with moniliform (or nearly so) cells (Yamada, 1938, fig. 13b), terminal spermatangia (Yamada, 1938, fig. 11a), and cystocarps with or without involucral filaments (Yamada, 1938, fig. 6c) contains *L. distenta, L. albicans* and *L. ceranoides*. *L. farinosa* is placed in section Farinosae, characterized by lateral carpogonial branches (Yamada 1938, fig. 15; 16b, c), head-like spermatangial clusters (Yamada, 1938, fig. 16a), and cells of assimilatory filaments not moniliform (Yamada, 1938, fig. 15). Of these features, the attachment of spermatangia, the density of their arrangements and their location on the assimilatory filaments are without question the most reliable of the presently used taxonomic characteristics. However, the spermatangial characteristics are most useful for sectional discrimination. Features of the assimilatory filaments (such as the shapes of cells, and the branching patterns) appear to be good specific differences if ages of the filaments are taken into consideration. Certain features of the development of the carposporophyte appear to be stable in a small number of species where these features have been evaluated: whether there is an involucre or not, whether it is initiated and remains entirely beneath the cystocarp, or above the attachment of the carpogonial branch; whether the carposporangia are formed in terminal cells only, or in a row of cells. Careful observations need to be made on a large number of specimens

in a larger number of species in order to judge the stability of these features. Vegetative features must be correlated not only between species but between gametophytes, for as shown in this paper, there are differences between gametophytes in *L. albicans*. Moreover, most of the studies in this paper were conducted on herbarium material; freshly collected and preserved material may show features that are lost upon drying; certainly liquid-preserved material reconstitutes and stains much more clearly than dried material.

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LEGENDS

Figs. 1-7. - *Liagora distenta*. Figs. 1-4, *L. versicolor* var. A. Fig. 1. Specimen with a percurrent axis. Fig. 2. Specimen with many finely divided, needle-like ultimate branches. Fig. 3. Specimen from Cadiz showing several leading axes. Fig. 4. Specimen from "Barbarie" showing a single main axis. Figs. 5-7. *L. versicolor* var. B. Fig. 5. Specimen showing notes written by Lamouroux and plant with a single main axis. Fig. 6. Dichotomously branched specimen. Fig. 7. Plant with several leading axes, resembling *Gracilaria* sp. in branching pattern (and texture). (All specimens, CN).

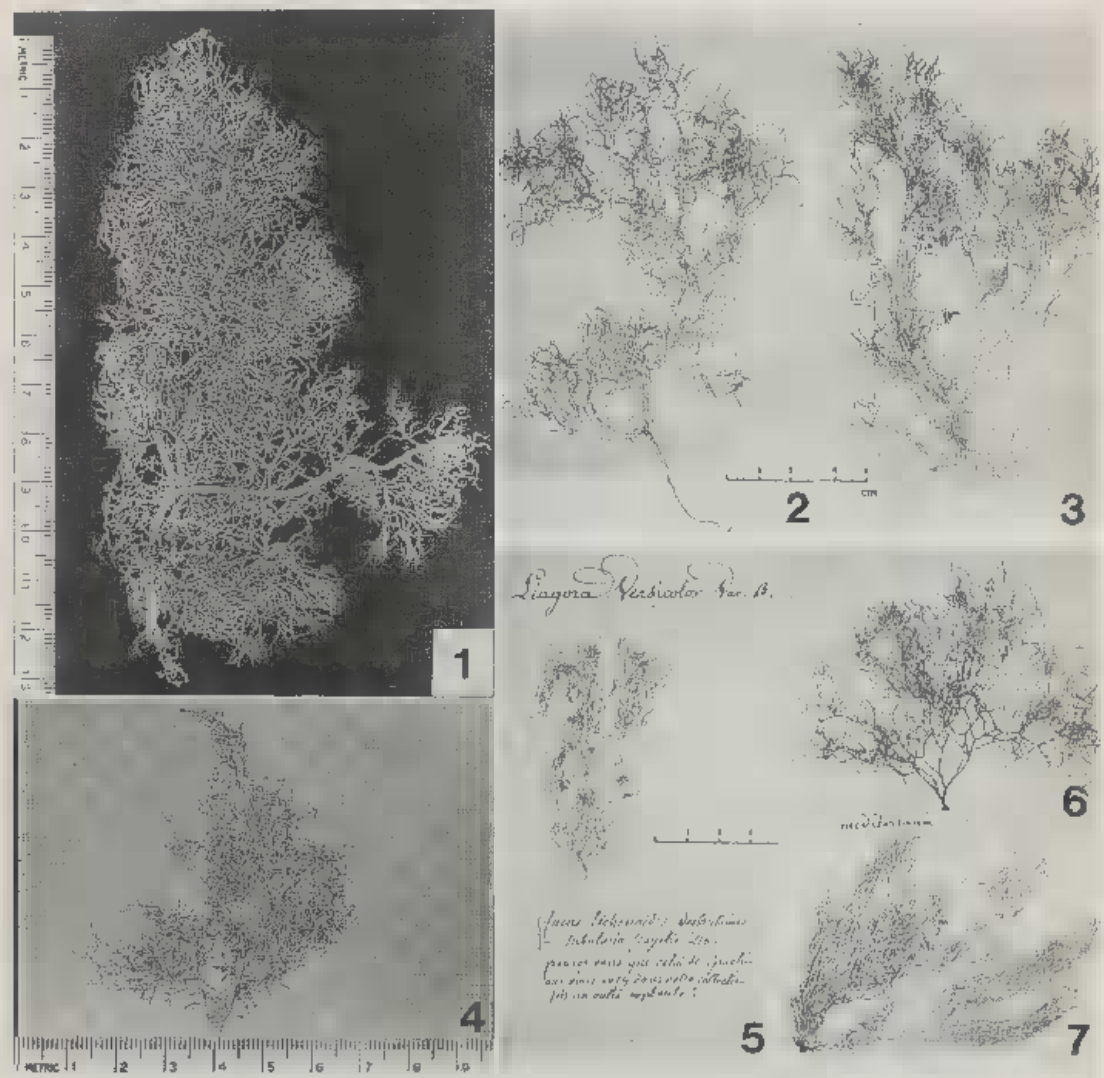
Figs. 8-11. - *Liagora distenta*. Fig. 8. *L. versicolor* var. C, a densely branched plant. Fig. 9. A dichotomously branched plant with a more open branching pattern. Fig. 10. One of several specimens queried as being "Tubularia fragilis". (All specimens in Figs. 8-10 in CN). Fig. 11. *Liagora distenta*. A recently collected specimen which is representative of the species. CANCAP 3161, east coast of Lanzarote, Macaronesia (BISH ex L).

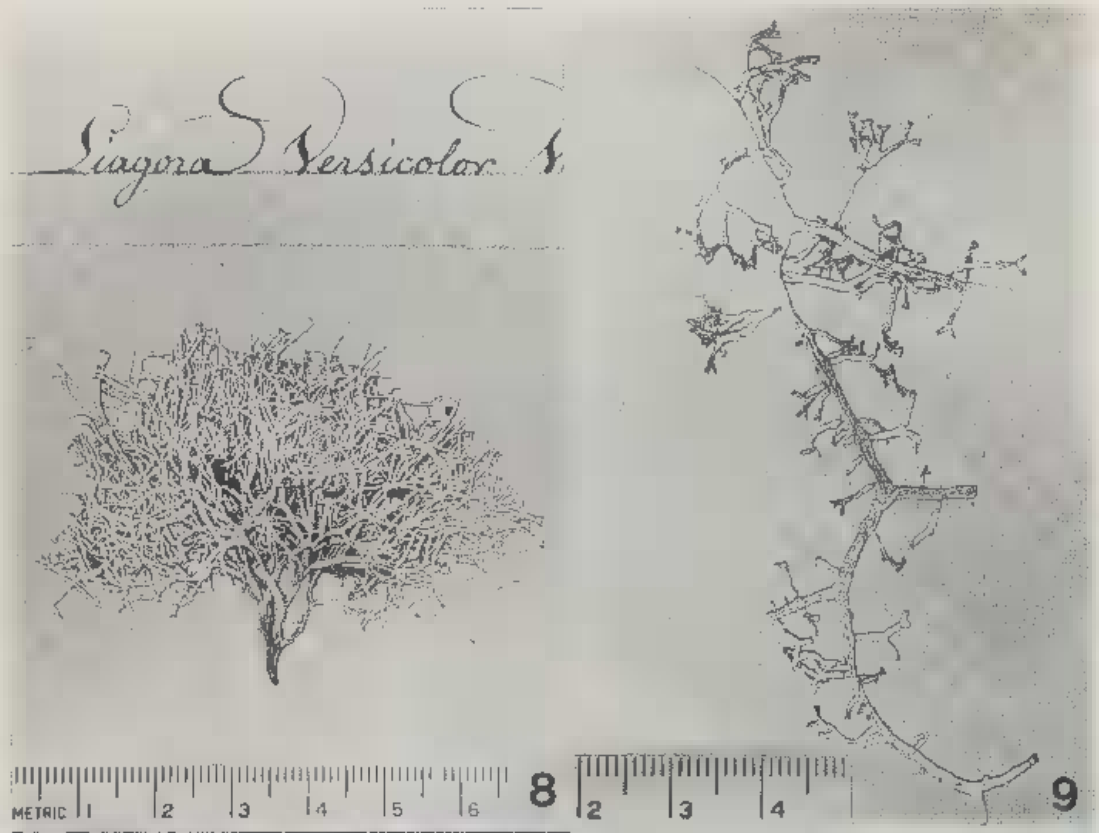
Figs. 12-15. - *Liagora ceranoides*. Fig. 12. Holotype from St. Thomas Island, Virgin Islands (CN). Fig. 13. Holotype of *L. leprosa* from Vera Cruz, Mexico (LD 32285). Fig. 14. Holotype of *L. opposita* from Florida (LD 32296). Fig. 15. Specimen (Abbott 11939) in BISH) from Light Princess, St. Croix, Virgin Islands that resembles *L. opposita*.

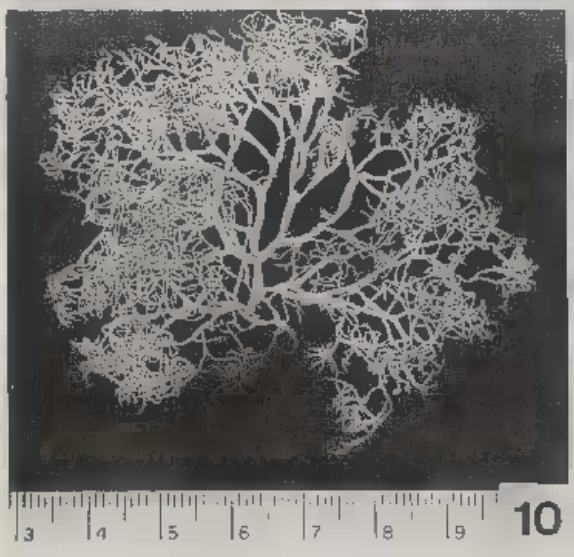
Figs. 16-21. *Liagora albicans*. Fig. 16. Syntype (Chauvin herbarium), showing relatively densely branched basal portion. Fig. 17. Portion of holotype of *L. decussata*, from Cape Verde, (Montagne herb., PC). Fig. 18. Lectotype of *L. ceylonica* (BM) from Ceylon (Sri Lanka). Fig. 19. *L. maxima* from Pupukea, Hawaii (Abbott 16276), a rather typical specimen. Fig. 20. *L. maxima*, intertidal from Kahanahaiki, Hawaii (Abbott 16450), showing pinnate branching and broken calcification along branches. Fig. 21. *L. maxima*, subtidal at 8-10m depth, from Makua, Hawaii showing thickly matted branches only obscurely pinnately branched.

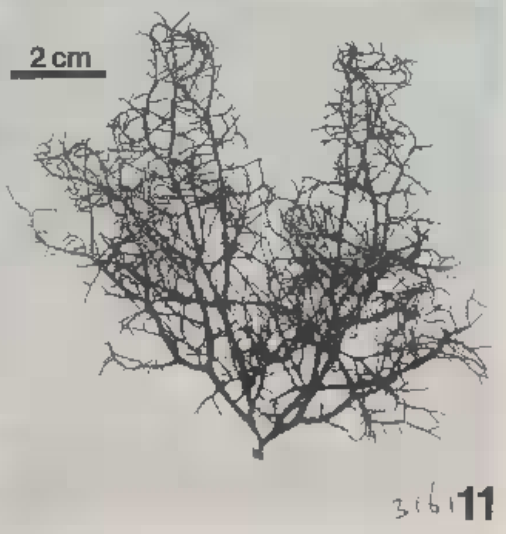
Fig. 22. - *Liagora aurantiaca*. Basal portion of a hydroid (CN). Figs. 23-25. *Liagora farinosa*. Fig. 23. Holotype of *L. farinosa* from the Red Sea (CN). Fig. 24. Holotype of *L. cliftonii* (BM) from Australia. Fig. 25. Holotype of *L. cayohuesonica* (BM) from Key West, Florida.

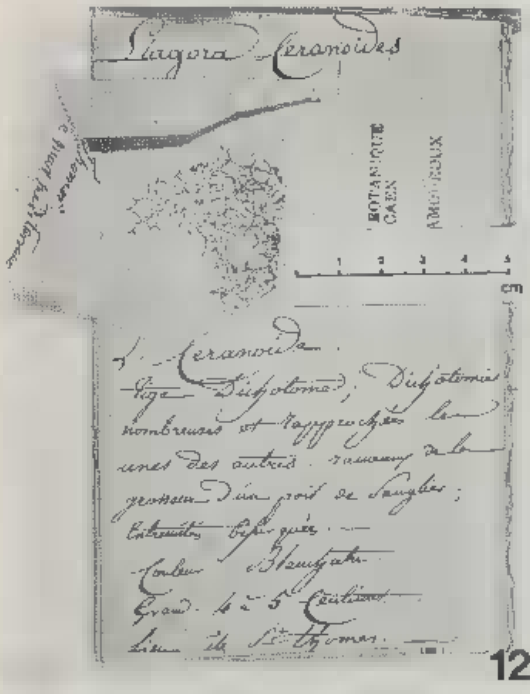
Figs 26-29. - *Liagora farinosa*. Fig. 26. Syntype of *L. farinosa* f. *pinnatiramosa* (BISH ex SAP) showing dense pinnate branching and coarse branchlets. Fig. 27. Lectotype of *L. crassa* (BM) from Flat Island, Mauritius, showing moderate pinnate branching. Fig. 28. Lectotype of *L. corymbosa* (LD 32368) from Florida, a very little-branched morphotype of *L. farinosa*. Fig. 29. Holotype of *L. paniculata* (LD 32395), less coarse and more calcified than most specimens of *L. farinosa*.











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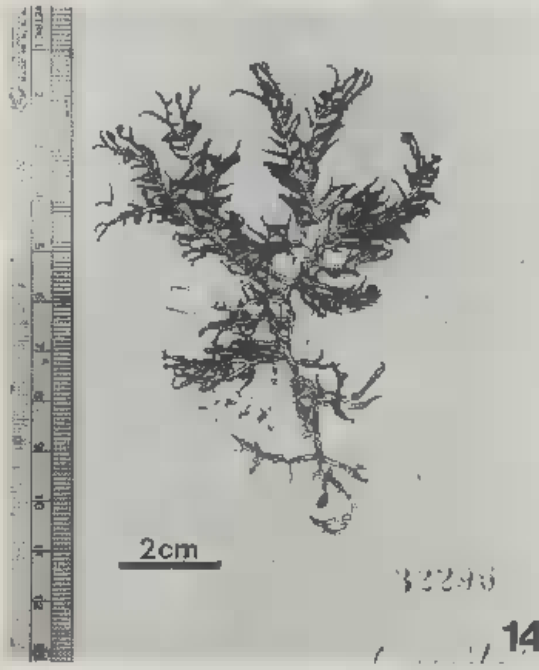

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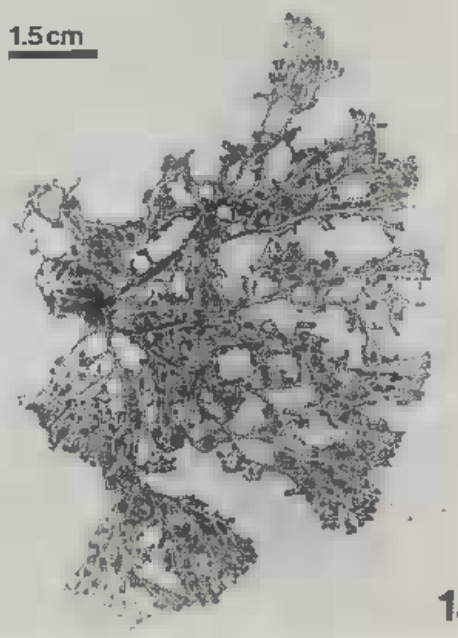

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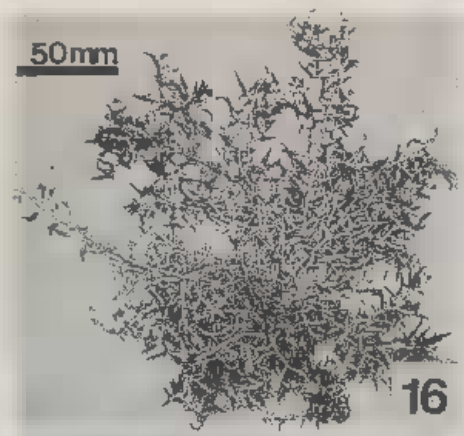

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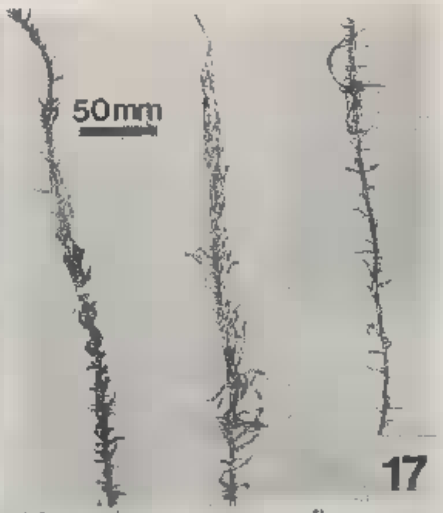

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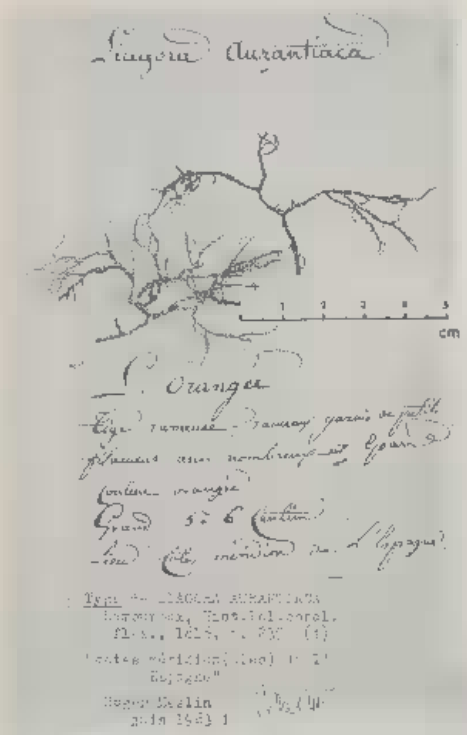

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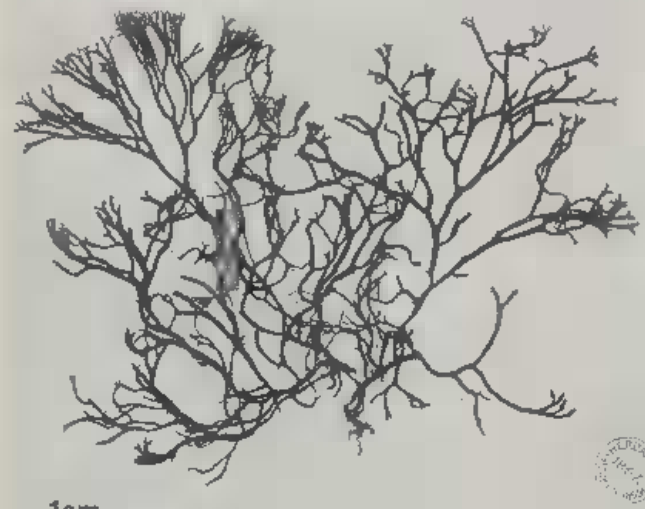

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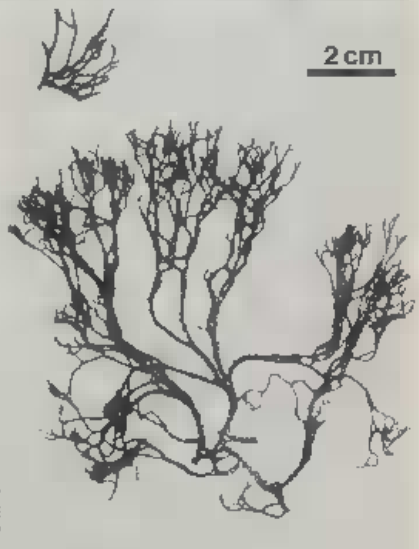

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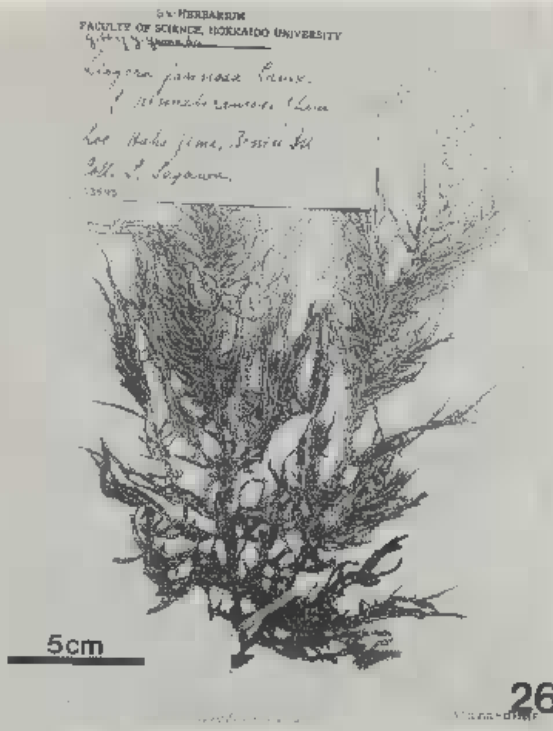

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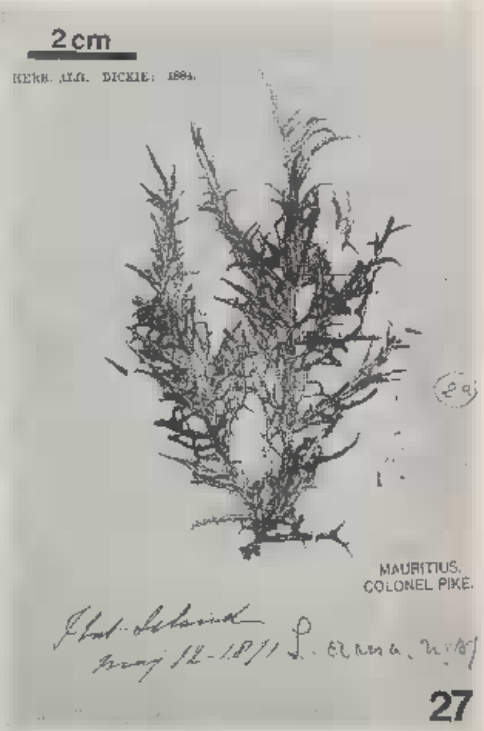

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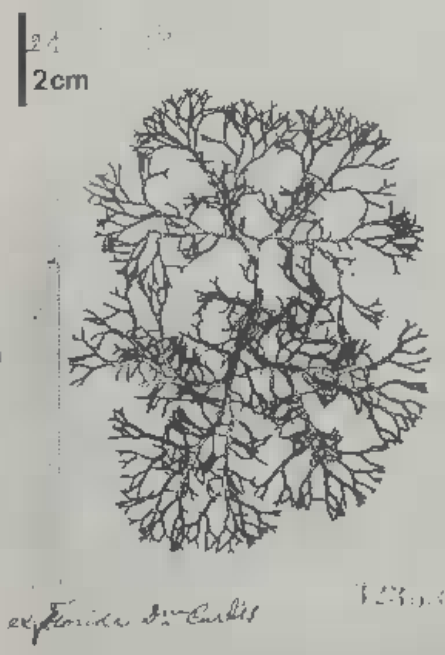

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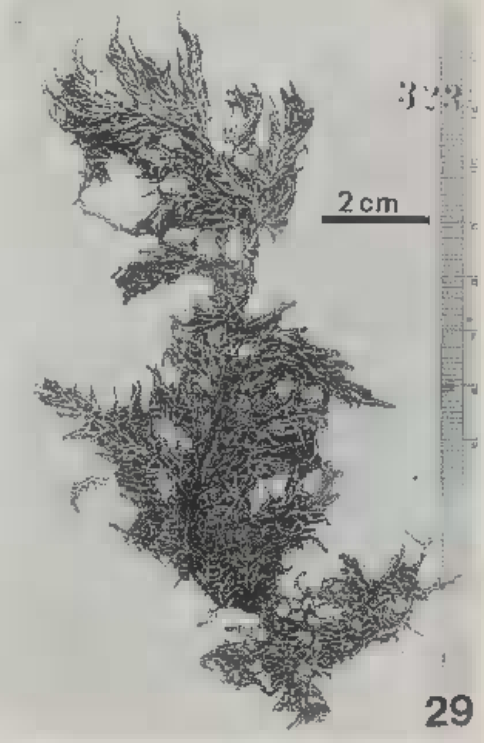

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